STUDIES ON THE TREMATODE GENUS PARAMONOSTOMUM LÜHE, 1909 (DIGENEA: NOTOCOTYLIDAE) [1]

HORACE W. STUNKARD

The American Museum of Natural History, Central Park West at 79th Street, New York, New York 10024

The genus *Paramonostomum* was erected by Lühe (1909) with *Monostoma alveatum* Mehlis in Creplin, 1846 (syn. *Monostoma alveiforme* Cohn, 1904) as type. The species had been included by Monticelli (1892) in the genus *Notocotylus* Diesing, 1839, but Lühe predicated that it is not congeneric with *Notocotylus triserialis* Diesing, 1839, type of *Notocotylus*. The species, *P. alveatum,* has been reported from a large number of birds including *Anas* spp., *Anser anser, Nyroca marilla, Oedemia* spp., *Somateria mollissima, Cygnus* spp., *Branta* spp., and *Clangula hyemalis.* Some 20 additional species of *Paramonostomum* have been described but distinctions between certain of them are very tenuous.

One life-cycle, that of *P. alveatum,* was reported by Kulachkova (1954). The work was done at the marine station on Kandalaska Bay, in the southwest portion of the White Sea, longitude 33° East and latitude 65.5° North. *Hydrobia ulvae* was the intermediate host and harbored the asexual generations of the parasite. Mme. Kulachkova published two short papers (1961a, 1961b) on seasonal infection of the mollusks and on the biology of the larval stages of *P. alveatum.* I am indebted to Dr. Galtsoff, who graciously translated the Russian texts for me. The studies of Mme. Kulachkova were occasioned by the mass mortality of young eider ducks; in the period 22 June to 7 July, 1949, 321 chicks died from the infection. As many as 50,000 worms were found in a single bird. The parasites penetrated between the intestinal villi, with inflammation and destruction of the epithelium and membranes. Fourteen per cent of the *H. ulvae* in the tide-pools were infected and the cercariae, on emergence, encysted promptly on the shells of the snails from which they had emerged. The cysts were 0.155 mm. in diameter and the worms matured in 6–8 days in the birds. The tide-pools had sandy-gravelly bottoms and the eider chicks, less than two weeks old, fed in these tide-pools where the shells of the hydrobias carried from 10 to 25 cysts per snail. Birds older than two weeks, fed in *Fucus* and mussel beds where the hydrobias were rare or absent, and birds older than two weeks survived. In the examination of 5427 snails over a four-year period, the rate of infection varied from 3.3% to 12%, with the greatest incidence in July and August. Shedding of the larvae began at water temperature of 23° and massive discharge in the range 23° to 26°. This was usually in the last week of June and first 10 days of July, although the dates varied with weather conditions, but this was the time when the eider chicks were feeding in the tide-pools.

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Miriam Rothschild (1938) had studied the cercariae of the notocotylid trematodes and described six species of these cercariae from the snails, *Peringia ulvae* and *Hydrobia ventrosa*. They were assigned to three different groups, based on the form of the excretory system: the MONOSTOMI group, in which the anterior transverse portion of the vesicle is a closed tubular circuit situated posterior to the median eye-spot and cerebral ganglion; the IMBRICATA group, in which the anterior portion of the vesicle forms a loop, between the eye-spots, which passes anterior to the median eye-spot and cerebral ganglion; and the YENCHINGENSIS group, in which there is an unpaired finger-like diverticulum which extends anteriad from the transverse portion of the vesicle.

Stunkard (1965) reported on the examination of more than 4000 specimens of *Hydrobia salsa* (Pilsbry, 1905) taken from brackish-water ponds, near Woods Hole, Massachusetts, and the discovery of at least four species of notocotylid cercariae, including the larval stages of *Paramonostomum alveatum*. The study has been continued and a fifth notocotylid species has been identified (Stunkard, 1966a). Two species have Yenchingensis type excretory systems; the metacercariae develop in the intestinal caeca of chicks and of domestic and eider ducklings, and belong to the genus *Notocotylus*. One of these species is identical with *Notocotylus minutus* Stunkard, 1960 and the other is described as a new species (Stunkard, 1966b). One of the five cercariae belongs to the Imbricata Group; it develops in the bursa Fabricius of chicks and domestic ducklings and may be identical with *Uniserialis gippyensis* Burton, 1958. The two other species have *Monostomi* type excretory systems; the metacercariae develop in the intestine of chicks and both domestic and eider ducklings, and belong to the genus *Paramonostomum*. One is identified as *P. alveatum;* and the other is *Paramonostomum parvum* Stunkard and Dunihue, 1931.

The methods for study of the *Paramonostomum* species are identical with those described for the species of *Notocotylus* (Stunkard, 1966b). The procedure is relatively simple. The infected snails were discovered by isolation; the larvae were studied alive, with and without the use of vital dyes. All stages were fixed and stained for subsequent study. Duboscq-Brasil and AFAG mixtures were used for fixation and specimens prepared as whole mounts were stained with Mayer's paracarmine, Semichon's acetic carmine, or Ehrlich's acid haematoxylin. Adult worms, sectioned serially in transverse and frontal planes, were stained with haematoxylin and erythrosin. Snails were isolated singly and metacercariae, encysted on the light side of the container, were fed at two-day intervals to rats, mice, hamsters, young herring gulls, chicks and both domestic and eider ducklings. The eider chicks were provided through the kindness of Mr. Walter Welch and his associates on the staff of the U. S. Fish and Wildlife Service, Boothbay Harbor, Maine. The snails were killed to identify the larval stages and the final hosts were killed to recover the developing and sexually mature worms. No infection was obtained in a mammalian species. Both species of *Paramonostomum* developed to maturity in chicks and in both eider and domestic ducklings, but sexually mature worms were not recovered from gulls. The intestine of a gull killed two days after the ingestion of about 200 metacercariae contained a few dead, excysted worms. Three live, juvenile specimens, identified as *P. parvum,* were recovered from the intestine of another gull fed metacercariae on 29 June, 1964, and autopsied 22 July, 1964.

The worms were the same size; fixed and stained they are 0.33 mm. long and 0.18 mm. wide, with very large ovaries and testes, but without eggs in their uteri. The two species of *Paramonostomum* are distinguished primarily by differences in size and size of organs. There are constant and apparently significant differences in sizes of cercariae, metacercariae and sexually mature adults. Twelve specimens of *P. alveatum* were left August 30, 1966, for several hours in pond-water and a large number of eggs were expelled by the worms. Three days later six young laboratory-reared *H. salsa* were placed in the dish with the eggs and were observed to eat some of them. The snails were then removed to fresh pond-water and a snail sacrified on October 3, 1966, contained rediae, some of which contained developing cercariae. The experimental infection of laboratory-reared *H. salsa* completes the life-cycle and confirms the earlier observations. The findings of the present study confirm the account of Mme. Kulachkova on *P. alveatum*.

Descriptions

Paramonostomum alveatum (Mehlis in Creplin, 1846) (Figs. 4–6)

Previous accounts include the inadequate redescription of the original specimens by Monticelli (1892), the brief statement by Lühe (1909) when he erected the genus *Paramonostomum,* and the account by Kossack (1911).

Adult (Fig. 4)

The worms are ovate, rounded posteriorly, more pointed anteriorly. Typically, the edges of the body are turned ventrad and mediad, so the venter forms a cupuliform cavity, which suggested the specific name, *alveatum.* The opening is smaller than the outline of the body. Fixed and stained sexually mature specimens measure 0.50 to 0.85 mm. in length and 0.40 to 0.53 mm. in greatest width, which is in the posterior half of the body. Under pressure of a coverglass, the dimensions of living worms are much greater. The cuticula appears to be smooth, but examination of living specimens under high magnification discloses exceedingly minute, closely set spines, arranged in parallel rows, on the ventral surface. The musculature of the body wall is weak and movement is slight or sluggish. The pigment from the ocelli of the cercaria persists in the parenchyma of the anterior end of the body. The oral sucker is 0.06 to 0.065 mm. in diameter; the esophagus is short, about the length of the oral sucker; the caeca are dorsal in location and follow the lateral contours of the body; they turn mediad at the anterior ends of the testes, pass between the testes and ovary, and terminate blindly behind the level of the gonads. As noted by Rothschild (1941, p. 363, fig. 1), "it is well known that in mature notocotylid trematodes the excretory vesicle becomes greatly complicated." Essentially, large, ramifying dendritic branches arise from the lateral and medial sides of the ring formed by the fusion of the collecting ducts of the cercaria, and constitute a complex reticulum that permeates the parenchyma of the body. The bladder, situated posterior to the ring, opens to the surface by a dorsal pore near the caudal end of the body.

The testes are oval, lobed organs, situated in the extracaecal areas at the poste-

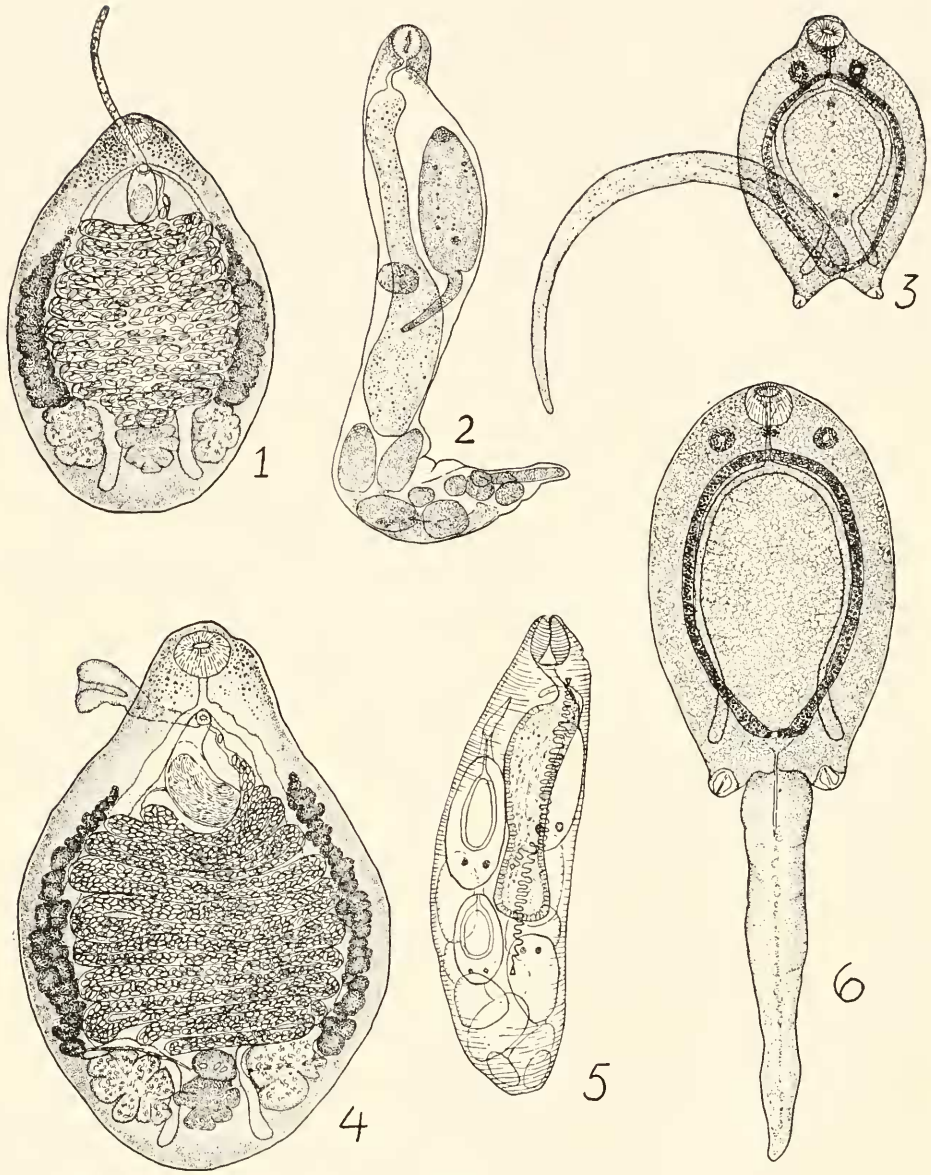

FIGURE 1. *Paramonostomum parvum*, adult specimen, ventral view, from eider duck; worm, 0.37 mm. long.

FIGURE 2. *P. parvum*, redia, pressed specimen, 0.93 mm. long.

FIGURE 3. *P. parvum*, cercaria, ventral aspect, fixed without pressure in hot whirling solution (Duboscq-Brasil), body, 0.17 mm. long.

FIGURE 4. *P. alveatum*, adult specimen, ventral view, from eider duck; worm, 0.75 mm. long.

FIGURE 5. *P. alveatum*, redia, fixed without pressure, 0.82 mm. long.

FIGURE 6. *P. alveatum*, cercaria, ventral aspect, fixed under pressure of coverglass, body 0.32 mm. long.

rior end of the body. They measure 0.12 to 0.18 by 0.10 to 0.14 mm. in diameter. Sperm-ducts arise at the anteromedian faces and unite in front of Mehlis' gland to form the vas deferens which passes anteriad, dorsal to the uterine coils. About one-third of the body-length from the anterior end, the duct enlarges to form a large, coiled, external seminal vesicle, the last loop of which extends forward on the right side of the cirrus sac. The cirrus sac is curved, short and broad, 0.16 to 0.24 mm. long and 0.10 to 0.13 mm. wide; the posterior portion contains the large internal seminal vesicle; the pars prostatica is short, and the cirrus is eversible (Fig. 4). The ovary is median, between the testes. It is a variably lobed organ, 0.08 to 0.15 mm. in diameter. The oviduct arises at the anterodorsal face of the ovary and receives a short, common vitelline duct as it enters Mehlis' gland, which is smaller and immediately anterior to the ovary. Mehlis' gland contains the ootype, in which the eggs are formed. The initial coils of the uterus are filled with spermatozoa. There are 10 to 12 transverse uterine loops that occupy the intercecal area posterior to the cirrus sac. They are ventral to the digestive caeca and in pressed specimens the vitellaria are almost contiguous with the uterine loops. The metraterm is ventral to the cirrus sac and about one-half its length. The vitellaria are extracaecal and extend from the testes to the level of the cirrus sac. The eggs are operculate, have long polar filaments, measure 0.019 to 0.021 by 0.011 to 0.012 mm., and are embryonated when passed.

Redia (Fig. 5)

The rediae are vermiform, cylindrical to sausage-shaped, and vary in size from young, colorless individuals with small germ balls to large, gravid rediae that may extend to a length of 1.20 mm., and when retracted may be 0.50 mm. in width. The size of the redia is largely determined by the number and size of the progeny in it. The large rediae are golden-yellow to orange in color. The body has annular and longitudinal muscles and when the longitudinal muscles are contracted, the wall has a crenate margin. The pharynx increases to 0.055 mm. in diameter and the esophagus is about the same length. In young rediae the intestine may extend more than one-half the length of the body, but it becomes relatively shorter as the redia is filled with offspring. The intestine is filled with decomposing snail tissue, yellow droplets and blackish amorphous material. The excretory pores are lateral, in the posterior half of the body. From each pore a common duct passes forward for a short distance and divides into anterior and posterior branches, each of which terminates in a flame-cell. The collecting ducts are coiled and are enclosed in straight-walled sinuses as described by Rothschild (1935).

Cercaria (Fig. 6)

The cercariae leave the rediae before they are mature and complete their development in the haemal sinuses of the snail. They emerge from the snails principally between 10 AM and 2 PM, and swim ordinarily for one to three or four hours. They encyst on the shell or operculum of the snail from which they emerged or on any hard surface. When irritated, *e.g.*, placed in a solution of vital dyes, they may encyst at once. When swimming, the body is contracted, bent ventrally; the tail is extended and lashes violently. They are photosensitive and accumulate on

the light side of the container. The body is oval to ovate, more pointed anteriorly, convex dorsally and concave ventrally; contracted it is circular, 0.20 to 0.25 mm. in diameter; elongated it may be 0.38 by 0.15 mm. The tail is simple, 0.20 to 0.50 mm. long and when extended it is 0.02 to 0.03 mm. wide at the base. When the body is extended the tail is contracted and *vice versa*. The posterolateral ends of the body bear eversible and retractile locomotor appendages, 0.020 to 0.025 mm. in diameter; when the body is extended they are close together, separated only by the base of the tail which is ventral to them; when the body is retracted they are at the posterior, dorsolateral corners. While in the redia, the cercariae have only two ocelli, with scattered pigment around the eye-spots, but by the time of emergence often there is a third, median, ring-like condensation of pigment between the ocelli, and dendritic strands of pigment extend posteriad along the digestive caeca. The ocelli are 0.018 to 0.020 mm. in diameter; they are provided with lenses and are situated dorsal and anterior to the ganglia of the nervous system. The parenchyma becomes filled with unicellular cystogenous glands; the secretion is in the form of bacilliform rods, 0.003 to 0.004 mm. in length and about one-half as wide. The oral sucker is 0.038 to 0.045 mm. in diameter; the esophagus is about the same length and crosses the excretory ring dorsally, whereupon it opens into the caeca. The caeca are dorsal and medial to the excretory ring as they pass posteriad, but near the posterior end of the body they turn laterad across the ring and end blindly as shown in the figure. The development of the excretory system of the cercaria agrees completely with the account of Rothschild (1935) on *C. ephemera* Lebour, 1907. In young cercariae the excretory pores are on the sides, near the middle of the tail, but in mature larvae, the portion of the system in the tail atrophies and a new excretory pore develops from the dorsal wall of the excretory bladder. The ring, formed by the coalescence posteriorly and anteriorly of the collecting ducts, is filled with concretions. In the posterior part of the ring there may be four to six concretions at any level, while in the anterior part of the ring the concretions may be disposed in a single row. They measure 0.003 to 0.006 mm. in diameter and often two or three are fused.

Metacercaria

In encysting, the cercaria attaches by the oral sucker; the body is contracted to circular form, and the cystogenous material is extruded on all sides. As the secretion hardens, the tail, which is left outside, lashes itself free and the cyst, 0.15 to 0.16 mm. in diameter, is firmly attached to the substratum. The cyst wall is relatively impermeable and resists desiccation; the larva moves in the cyst and if not dried, remains infective for a long period, weeks, possibly months.

Paramonostomum parvum Stunkard and Dunihue, 1931
(Figs. 1–3)

This species, described originally from specimens found in the intestine of an unidentified duck, was recovered after feeding metacercariae to laboratory-reared eider and domestic ducklings and to day-old chicks. The asexual generations were found in *Hydrobia salsa* taken from Nobska and Oyster Ponds, brackish-water areas that communicate with Vineyard Sound, near Woods Hole, Massachusetts.

The specimens of experimental infection agree completely with the description of worms of natural infection as reported by Stunkard and Dunihue (1931).

Adult (Fig. 1)

The worms measure 0.25 to 0.50 mm. in length and 0.20 to 0.35 mm. in width. Only much flattened specimens exceed 0.50 mm. in length. In the original report, the presence of spines on the cuticula was regarded as doubtful. With an abundance of material, it has been possible to observe the presence of exceedingly minute, closely-set spines on the ventral surface of the body. The spines are arranged in fine, parallel rows. They are not visible on fixed and stained specimens, but on living worms under high magnification they can be resolved by careful focussing.

Redia (Fig. 2)

The rediae closely resemble those of *P. alveatum;* they occupy the haemal sinuses of the snail and grow to a size of 0.65 by 0.13 mm. or 0.75 by 0.10 mm. Daughter rediae emerge from the parental rediae while very small, much smaller than the cercariae when they emerge, and while small they are active and migratory. As the body cavity becomes filled with germ-balls and developing cercariae, the rediae become more sluggish. The pharynx increases to a diameter of 0.035–0.042 mm., and when pressed may measure 0.05 mm. in diameter. The esophagus is approximately as long as the pharynx and the caecum varies with the size of the redia. In young specimens the caecum is long, often more than one-half the body length, but is relatively shorter as the redia enlarges. The caecum is filled with partially digested snail tissue, yellow droplets and amorphous, blackish material. The young rediae are colorless but as they grow they become more and more filled with orange-yellow material. The excretory system is identical with that of the redia of *P. alveatum.*

Cercaria (Fig. 3)

The cercariae differ from those of *P. alveatum* principally in size. They emerge at about the same time of day, have the same swimming movements, accumulate on the light side of the container, and encyst on the shells of the snails or other hard surface in the course of one to three or four hours. They emerge from the rediae while still immature and at this stage have considerable dark pigment around the ocelli and in the anterior third of the body. On emergence from the snail, the body is oval to ovate, more pointed anteriorly, convex dorsally and concave ventrally; contracted it is circular, 0.14 to 0.16 mm. in diameter; extended it may be 0.30 by 0.10 mm. The tail is simple, slender; it varies from one-half to three times the length of the body. The locomotor appendage pits at the posterolateral ends of the body are smaller than those of *P. alveatum* and diverge at an angle in specimens killed without pressure in whirling, hot, fixing fluids (Fig. 3). The ocelli are dorsal and anterior to the cephalic ganglia and measure about 0.015 mm. in diameter; they are provided with lenses. The oral sucker is 0.029 to 0.036 mm. in diameter; the esophagus is approximately the same length; the caeca follow the

lateral contours of the body until they turn laterad and cross the excretory ring dorsally, near the posterior end of the body. The body is filled with cystogenous cells; the secretion appears as bacilliform rods, 0.002 to 0.003 mm. long and about one-half as wide. There are 12 to 15 cells between the caeca in a transverse section through the middle of the body. The excretory system develops as in all notocotylid cercariae; the ring passes posterior to the ganglia and ocelli and is filled with concretions; they vary from 0.003 to 0.006 mm. in diameter. On either side, a recurrent tubule passes posteriad from the anterolateral faces of the ring; the recurrent tubule bears tufts of long cilia and near the middle of the body divides into anterior and posterior branches. Each branch bears three clusters of flame-cells, probably three in each cluster, but not all cells have been observed, as the cystogenous cells begin to fill with secretions before all the cells and tubules of the midbody are recognizable.

Metacercaria

The cercariae encyst promptly if irritated by agitation of the water or the presence of toxic substances, *e.g.*, solutions of vital dyes; otherwise they may swim for one to three or four hours. They encyst on the operculum or shell of the snail or any hard surface, including the wall of the container, always on the side toward the light. The cysts measure 0.13 to 0.14 mm. outside diameter and 0.11 to 0.12 mm. inside diameter. A specimen was fixed while encysting on a slide; the secretion had produced a thin, flexible membrane and outside the membrane there was a sheet of seta-like projections of cystogenous material, 0.030 mm. long and 0.003 mm. in diameter.

Discussion

Rothschild (1941) reported efforts, continued for five years, to solve the life-histories of the notocotylid cercariae that parasitize *Peringia ulvae*. Six species of larvae were isolated and cysts were fed to laboratory-reared ducklings. Three of the species belonged to the Monostomi group and three to the Yenchingensis group of cercariae. All attempts to obtain adult worms from the Monostomi cercariae were negative but she reported (p. 363), "Two species of the Yenchingensis sub-group, however, developed in the intestinal ceca of the ducks, into flukes of the genus *Paramonostomum*." Rothschild noted with some surprise that one cercaria of the Yenchingensis group (Szidat and Szidat, 1933) and one of the Monostomi group (Yamaguti, 1938) had been reported to develop into the same species of adult, *Notocotylus attenuatus*. Although Rothschild obtained adult specimens referred to the genus *Paramonostomum*, the specific identity of the specimens was not determined. Kulachkova (1954) did not assign the cercariae of *P. alveatum* to one of the larval groups. The recent studies of Odening (1966) are particularly interesting; he reported that the cercariae of *Notocotylus ephemera* (Nitzsch, 1807); *Notocotylus noyeri* Joyeux, 1922; *Notocotylus pacifer* (Noble, 1933); *Notocotylus ralli* Baylis, 1936; and *Notocotylus regis* Harwood, 1939, all of which develop in fresh-water, pulmonate snails, belong to the Monostomi group of cercariae; whereas the cercariae of *Catatropis verrucosa*, which also develop in fresh-water pulmonates, *Segmentina nitida* and *Gyraulus albus*, belong to the Imbricata group. From the studies of Stunkard (1960) on the life history of

Notocotylus minutus and (1966b) on *Notocotylus atlanticus,* it appeared that cercariae of species of *Notocotylus* belong to the Yenchingensis group and mature in the digestive caeca of birds, whereas the cercariae of *Paramonostomum* belong to the Monostomi group and develop in the lumen of the intestine. However, the statements of Rothschild and Odening do not permit such a correlation between larval type, developmental site, and generic allocation, and the significance of the larval groups remains obscure and equivocal.

The genus *Paramonostomum* contains some 20 described species, but the distinctions between certain of them are very tenuous. Existing descriptions are based almost entirely on morphology of adult specimens, especially on position of the genital pore and extent of the vitellaria. Some species are based on the description of a single individual, without adequate consideration for the variation that always and inevitably occurs. It is admitted that morphological divergence results from differences in age and degree of maturity, from extension and retraction of entire specimens or of particular regions of the body, from the accumulation of reproductive products and from procedures of examination, fixation and preservation, especially the degree of flattening under pressure of a coverglass. Measurements made on living specimens may differ significantly from those made on the same individuals after fixation and staining. Moreover, although specificity in the molluscan host may be relatively restricted, representatives may develop in final hosts as diverse as birds and mammals, with substantial structural modifications. *Paramonostomum echinatum* Harrah, 1922 and *Paramonostomum pseudalveatum* Price, 1931, were described from muskrats, *Ondatra zibethica,* whereas all other species are from avian hosts. Swales (1933) reported, without description, the finding of *P. pseudalveatum* in *Branta canadensis* taken in Nova Scotia. Lal (1936) included *P. parvum* in a new genus, *Neoparamonostomum,* based on *Paramonostomum ionorne* Travassos, 1921 and characterized by the location of the genital pore and extent of vitellaria. Harwood (1939) discussed the genus *Paramonostomum,* suppressed *Neoparamonostomum* as a synonym of *Paramonostomum,* and considered the problems of generic and specific identity. He noted that *Paramonostomum* differs from other notocotylid genera only in the absence of ventral glands, and since these glands are frequently very difficult to locate, it is possible that some of the species now assigned to *Paramonostomum* may ultimately be found to belong elsewhere. The species of *Paramonostomum* were arranged in two groups: the *Alveatum* group, short, oval, with vitellaria extending to the level of the cirrus sac, to contain the species, *alveatum, pseudalveatum, parvum,* and possibly *ionorne;* and the *Elongatum* group, with elongate, spatulate bodies, suggestive of *Notocotylus,* with a space between the vitellaria and the cirrus sac, to contain all the other species. Although the observation of Harwood has merit, Dunagan (1957, p. 581) commented, "Neither of these groups, however, possesses characters inherent to one but not both. The division is, therefore, of little value for systematic purposes." Harwood supplemented the description of *P. parvum* by the study of specimens from the Helminthological Collection of the U. S. National Museum, including No. 39598 from the intestine of a blue goose, *Chen caerulescens,* collected by A. M. Fallis in Ontario, Canada, and No. 43148 from the intestine of the American golden-eye, *Glaucionetta clangula americana,* collected by D. K. Coburn at the Migratory Bird Refuge, Brigham, Utah. The worms meas-

ured 0.69 to 0.80 mm. in length and 0.46 to 0.50 mm. in width. Harwood stated (p. 337), "The specimens on which the present redescription is based are, if judgment is based on size alone, more similar to *Paramonostomum alveatum* than to *P. parvum.* They are referred to the latter species, because in the writer's opinion size is an extremely variable character in trematodes, and because both the distribution of the vitellaria and position of the genital pore are as described and figured by Stunkard and Dunihue; they differ in these respects from *P. alveatum* as figured by both Lühe (1909) and Kossack (1911). These structural characters are regarded as more important than size differences." Harwood assigned the species reported by Swales (1933) to *P. parvum.*

The studies of Harwood raise questions of specificity in the genus *Paramonostomum.* The position of the genital pore relative to the bifurcation of the digestive tract, and the extent of the vitellaria are variable; indeed, Harwood observed (p. 336), that the location of the genital pore "may not be wholly reliable in specimens preserved in a contracted state, especially if the cephalic end is curved ventrad." Observation of living specimens discloses much variation in location of the genital pore as the anterior end of the body is extended and retracted. The description of *P. alveatum* by Kossack (1911) was based on material from a number of host species and the specimens varied from 0.78 to 0.90 mm. in length and 0.50 to 0.56 mm. in width. The genital pore was described as ventral to the intestinal bifurcation and the vitellaria occupied the middle third of the body. Concerning the vitellaria, Kossack stated (p. 564), "Doch ist ihre Erstreckung nicht ganz konstant, da sie häufig nach hinten bis zum Vorderrand der Hoden reichen." In the present study, the cercariae, metacercariae, and adults are referable to two different size groups. The adults of one group are less than 0.50 mm. in length and are identified as *P. parvum;* adults of the other group are 0.55 to 0.90 mm. in length and are identified as *P. alveatum.* If there were specimens of intermediate size, it would be feasible to include all in a single species, but since all were from the same intermediate host-species and developed in the same final host-species, the differences appear to be genetic. The specimens studied by Harwood agree with the larger of the present species and may belong to *P. alveatum.*

Examination of published descriptions in the light of the above considerations raises doubt concerning the validity of certain species. *Paramonostomum pseudalveatum* Price, 1931, from the muskrat, is very similar to *P. parvum* Stunkard and Dunihue, 1931, from an unidentified duck, whose life-cycle is reported in the present paper. The two species are virtually equal in size and shape; in both the cirrus sac is short and wide, with loops of the seminal vesicle and uterus extending beside the sac; the metraterm is short, not more than one-half the length of the cirrus sac; the vitellaria extend from the testes to the level of the cirrus sac, and the uterus has 8 to 11 transverse loops. *Paramonostomum pseudalveatum* has a larger oral sucker, larger gonads, larger cirrus sac and a somewhat more anterior location of the genital pore. If these features are the result of development in different hosts, the two species may be identical. Similarly, *Paramonostomum brantae* Bullock, 1952, agrees so completely with descriptions of *P. alveatum* that the two specific concepts merge and *P. brantae* falls in synonymy. Bullock (1952) noted the similarity and distinguished between the two species on the shape of the ovary in *P. alveatum,* which he recognized as an unreliable character, and the

larger cirrus sac of *P. brantae*. The figure of *P. brantae* shows the cirrus sac expanded and filled with spermatozoa. *Paramonostomum macrostomum* Ku, 1938, was described on a single specimen from *Fulica atra* taken at Soochow, China. A somewhat larger single specimen from the same host, *F. atra,* taken at Lucknow, India, was described by Baugh (1958) as *Paramonostomum fulicai. Paramonostomum nettioni* Baugh, 1958, from the common teal, *Nettion crecca,* is similar morphologically and is intermediate in size between *P. macrostomum* and *P. fulicai,* but information is inadequate to determine the specific status of these species. Two species, *Paramonostomum casarcum* from *Casarca rutila* and *Paramonostomum querquedulum* from *Querquedula circia,* were described by Lal (1936) in India. Each species was described from a single specimen. The worms are approximately the same size and morphological agreement is so complete and precise that specific distinction is highly questionable. An item of reported difference is the location of the genital pore, which in *P. casarcum* is at the posterior border of the oral sucker, whereas in *P. querquedulum* it is slightly anterior to the intestinal bifurcation. But the location of the pore shifts with extension and retraction of the anterior end of the body and with the orientation of the oral sucker. If the sucker is turned so that the mouth is subterminal, the esophagus appears short and bent and the pore apparently is farther forward. Moreover, the two species described by Lal (1936) are very similar to and may be identical with worms from ducks taken at Soochow, China, and described by Hsü (1935) as *Paramonostomum ovatum.* The description of *Paramonostomum microstomum* by Moghe (1932) is incomplete, the uterus is represented in diagrammatic manner and the locations of the ovary and Mehlis' gland are reversed. The specimens were from *Philomachus pugnax,* taken at Nagpur, India, and are similar to those described by Lal (1936). The single specimen from *Querquedula discors* taken in Mexico and described by Caballero (1942) as *Paramonostomum obtortum,* closely resembles the worms described by Lal (1936). A distinct group, characterized by long cirrus sac and short vitelline zones, includes *Paramonostomum actiditis* Cable, 1960, from charadriiform birds of Puerto Rico, and *Paramonostomum histrionici* Ching, 1962, from *Histrionicus pacificus* taken near Friday Harbor, Washington. Three other species are characterized by linear, spatulate bodies, very long cirrus sacs that extend to the middle of the body and short vitelline zones. They are *Paramonostomum elongatum* Yamaguti, 1934, from *Olor bewicki jankowskii* and *Olor cygnus* taken in Korea; *Paramonostomum bucephalae* Yamaguti, 1935, from *Bucephala clangula, Tadorna tadorna, Spatula clypeata* and *Nyroca marila mariloides,* taken in Japan; and *Paramonostomum malerischi* Dunagan, 1957, from the emperor goose, *Philacte canaganica,* taken in Alaska. The description of new species from single specimens is not commended and final determination of specific identity in the genus *Paramonostomum* may depend on the discovery of life-cycles and the description of larval stages.

Summary

The account of Mme. Kulachkova (1954) on the life-history of *Paramonostomum alvealtum* is confirmed. The asexual generations and larval stages of both *Paramonostomum alveatum* and *Paramonostomum parvum* occur in the prosobranchiate snail, *Hydrobia salsa,* found in brackish-water ponds near Woods Hole,

Massachusetts. Sexually mature worms have been obtained by feeding metacercariae to day-old chicks and laboratory-reared eider and domestic ducklings. Adult and larval stages of both species are described and figured. Problems of specific identity in the genus *Paramonostomum* are discussed.

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